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Control of green mold and sour rot of stored lemon by biofumigation with *Muscodor albus*

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Abstract

Control of postharvest lemon diseases by biofumigation with the volatile-producing fungus *Muscodor albus* was investigated. In vitro exposure to *M. albus* volatile compounds for 3 days killed *Penicillium digitatum* and *Geotrichum citri-aurantii*, causes of green mold and sour rot of lemons, respectively. Lemons were wound-inoculated with *P. digitatum* and placed in closed 11-L plastic boxes with rye grain cultures of *M. albus* at ambient temperature. There was no contact between the fungus and the fruit. Biofumigation for 24–72 h controlled green mold significantly, even when treatment began 24 h after inoculation. Effectiveness was related to the amount of *M. albus* present. In tests conducted inside a 11.7-m^3 degreening room with 5 ppm ethylene at 20 °C, green mold incidence on lemons was reduced on average from 89.8 to 26.2% after exposure to *M. albus* for 48 h. Ethylene accelerates color development in harvested citrus fruit. *M. albus* had no effect on color development. Biofumigation in small boxes immediately after inoculation controlled sour rot, but was ineffective if applied 24 h later. *G. citri-aurantii* may be less sensitive to the volatile compounds than *P. digitatum* or escapes exposure within the fruit rind. Biofumigation with *M. albus* could control decay effectively in storage rooms or shipping packages.

Keywords: Biofumigation; *Citrus*; Fumigant; *Geotrichum citri-aurantii*; Lemon; *Muscodor albus*; *Penicillium digitatum*; Postharvest; Sour rot; Volatile

1. Introduction

Harvested citrus fruit are very susceptible to wound infection by *Penicillium digitatum* (Pers.:Fr.) Sacc, which causes green mold of citrus (Sommer et al., 2002). Minimizing wounds on fruit, proper temperature management, and postharvest fungicide treatments are the main methods of reducing losses by this pathogen (Eckert and Eaks, 1989). Continuous use of fungicides such as imazalil, thiabendazole, and *o*-phenylphenol in citrus packing facilities in California has resulted in the appearance of *P. digitatum* isolates with multiple fungicide resistances within natural populations (Holmes and Eckert, 1999), which further complicates the management of green mold. In addition, maximum residue limits for imazalil, the most important fungicide in use, are lower in most citrus importing countries than in the United States (United States Department of Agriculture-Foreign Agricultural Service, 2004). Because of these constraints, new approaches to protect citrus fruit from diseases in domestic and foreign markets are of interest to the citrus industry.

Sour rot of citrus, caused by *Geotrichum citri-aurantii* Butler (syn = *Geotrichum candidum* Link), is another potentially devastating storage disease. Although less common than green mold, it can cause significant losses in high rainfall years. Sour rot is not controlled with the currently registered fungicides imazalil and thiabendazole,

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and only partially controlled by sodium *o*-phenylphenate, which is not commonly used due to risk of fruit injury (Eckert and Eaks, 1989). Sour rot can be partially managed by sanitation and minimizing fruit storage temperatures after harvest, but chilling injury to the fruit and temperature variations during transport and marketing limit the effectiveness of this approach. Inoculum from infected fruit may create large nests of infected fruit during storage and transportation.

There have been considerable efforts to develop methods to control fungal decay in citrus that are considered to be safer to consumers, workers, and the environment than the fungicides now in use. These include biological control (Janisiewicz and Korsten, 2002), low toxicity chemicals (Smilanick et al., 1997, 1999), and physical treatments such as heat and UV-C, which can enhance disease resistance (D'hallewin et al., 1993, 2000; Porat et al., 2000). Currently, the biofungicides Aspire and BioSave are registered for postharvest use on citrus in the United States (Janisiewicz and Korsten, 2002), although both have shown limitations in efficacy as stand-alone treatments for citrus fruit (Brown and Chambers, 1996; Brown et al., 2000; Droby et al., 1998). Because most alternative treatments need further efforts in research and development to be implemented, there is still a need in the citrus industry for effective and environmentally friendly means of postharvest decay control.

Biological fumigation, or biofumigation, with volatile compounds produced by the fungus *Muscodor albus* Worapong, Strobel, and Hess has shown promise for killing a wide range of storage pathogens and controlling fungal decay (Mercier and Jiménez, 2004). Biofumigation for 24 h or longer with rye grain culture of *M. albus* controlled brown rot of peaches, caused by *Monilinia fructicola*, and gray mold and blue mold of apple, caused by *Botrytis cinerea* and *P. expansum*, respectively (Mercier and Jiménez, 2004). Biofumigation of greenhouse soilless mix with rye grain culture of *M. albus* was also effective in controlling soil-borne diseases of vegetable seedlings (Mercier and Manker, 2005). *M. albus* was reported to produce 28 organic volatile compounds which together inhibited and killed various species of fungi, oomycetes, and bacteria (Strobel et al., 2001). The fungus, which is closely related to the endophytic fungus *Xylaria* (Ascomycetes), was isolated as an endophyte from a cinnamon tree (Worapong et al., 2001). *M. albus* is a sterile mycelium and can grow readily on ordinary culture media such as potato dextrose agar. The main objective of this research was to evaluate the potential of biofumigation with rye grain culture of *M. albus* to control green mold and sour rot of lemons, focusing on the biofumigant dose and treatment time required. Large-scale biofumigation of lemons during ethylene treatment of a storage room was also done to evaluate compatibility with the degreening process and potential for scaling up the treatment for commercial application.

2. Materials and methods

2.1. Fungal isolates

Muscodor albus isolate 620 was obtained from Dr. G. Strobel, Montana State University, and was described previously (Worapong et al., 2001). The fungus was grown on autoclaved rye grain as described previously (Mercier and Jiménez, 2004) and the fresh culture was used for the biofumigation experiments. In the case of large-scale experiments, air-dried rye culture was used after adding water at a 1:1 ratio (w/w). The air-dried rye culture of *M. albus* was shown to have disease control activity equivalent to fresh culture upon re-hydration when tested against blue mold of apple (J. Mercier, unpublished data).

Postharvest pathogens used in this study were *P. digitatum* isolate M6R, obtained from J.W. Eckert, and *G. citri-aurantii*, which was isolated from an infected lemon. The isolates were preserved as spore suspensions in 15% glycerol at −80 °C and re-cultured when needed. Inoculation methods were those recommended by Eckert and Brown (1986). The pathogens were grown on potato dextrose agar (PDA) at room temperature for 5–10 days. To make conidial suspensions of *P. digitatum*, the plates were flooded with water with 0.01% Tween 20 and rubbed gently with a glass rod. The resulting suspension was filtered through one layer of cheesecloth and the concentration was adjusted with a hemacytometer. Arthrospore suspensions of *G. citri-aurantii* were prepared similarly but were adjusted with a spectrophotometer to contain 1×10^8 arthrospores/ml.

2.2. In vitro effect of M. albus volatile compounds on P. digitatum and G. citri-aurantii

The effect of volatile compounds on the isolates of the postharvest pathogens used in this study was tested on PDA as described by Strobel et al. (2001). A strip of agar was removed across each plate to make a medium-free moat physically separating two areas with medium and preventing any metabolites from diffusing across the plate through the medium. After growing *M. albus* on one side of the plate for 7 days, a PDA agar plug (6 mm diameter) of a test pathogen culture was added to the other side before sealing with parafilm. Three replicate plates were used for each pathogen. Growth was rated after three days at 21–23 °C. Plugs that did not grow after three days were transferred to fresh PDA plates to assess their viability.

2.3. Control of green mold

Experiments were conducted with organically grown lemons cv. Eureka from California. Fruits were selected for absence of injuries and visible defects, to minimize

interference from natural infections. Lemons were placed in 11.4-L plastic boxes, each restrained in a 7-mm plastic weigh dish to immobilize the fruit. Each fruit was wound-inoculated on one location at the equator with a steel rod with a 2 mm long by 1 mm wide tip dipped in a conidial suspension of 10^5/ml. Each box was fumigated immediately or 24 h after inoculation by placing a plastic cup containing 30 g of *M. albus* grain culture within the box for periods from 24 to 72 h. The boxes were kept closed with a tight fitting, but not airtight, plastic lid. The control consisted of inoculated fruits in boxes without colonized grain. Different amounts of *M. albus* culture were tested by placing it with the fruit for a 24-h period beginning 24 h after inoculation with 10^5 or 10^6 conidia/ml. The boxes were kept at ambient air temperature (21–25 °C), and infection was measured after 7 days by counting fruit with developing lesions. Each experiment was conducted in a completely randomized design with 12–14 lemons per box, and three to four boxes per treatment.

2.4. Control of sour rot

Experiments for sour rot control were conducted as described above for green mold. In the first experiment, lemons were wound-inoculated with a suspension of 1×10^8 arthrospores/ml supplemented with 10 % lemon juice. Lemon juice was prepared by squeezing a fruit into a metal mesh to remove the pulp before adding it to the inoculum. The lemons were fumigated for a period of 24–72 h, beginning immediately or 24 h after inoculation, and the number of decayed fruit was estimated 14 days after inoculation. In the second experiment, the lemons were inoculated with an arthrospore suspension supplemented with 10 ppm cycloheximide to retard wound healing and with 100 ppm thiabendazole to prevent green mold from interfering with sour rot development (Eckert and Brown, 1986). In this experiment, fumigation for 24, 48, 72, and 120 h was initiated immediately after inoculation. The percentage of infected fruit was determined 4 and 7 days after inoculation.

2.5. Room fumigation for green mold control

Biofumigation in storage rooms during degreening was tested by placing inoculated fruit in two storage rooms of $1.8 \times 3.0 \times 2.1$ m in size that were maintained at 20 °C with 5 ppm of ethylene from a compressed cylinder. This work was conducted at the University of California Lindcove Citrus Research and Extension Center in Exeter, CA. Lemons were inoculated with *P. digitatum* (10^5 conidia/ml) as described previously and placed in bulk lots of about 140 fruit in each open plastic lemon storage box, or of about 100 fruit each in fiberboard carton. The lemon storage boxes were 33 cm wide, 27 cm deep, and 68 cm long. The top of the box was open, and the remainder of box was perforated by rectangular vents that comprised more than 50% of the box surface area. The fiberboard cartons were 28 cm wide, 26 cm deep, and 42 cm long. The cartons had a sleeve lid and when closed ventilation was composed of 20 round vents 3.5 cm in diameter with a total vented area of 2.6% of the surface area of the carton. There were three to five replicate boxes or cartons in each room. In one room, 10 kg of dry grain culture of *M. albus* was placed in open plastic trays and re-hydrated at a rate of 1:1 (w/w) with deionized water at the beginning of the degreening process. After 48 h, the ethylene treatment was stopped and colonized grain was removed. The percentage of infected fruit was evaluated after an additional 5 or 6 days of storage at 20 °C. The room fumigation experiment was performed twice with the open plastic boxes. The fiberboard cartons were included only in the second experiment.

2.6. Statistical analyses

The analysis of variance of percent infection data and their arscine transformation was performed using the NCSS software version 6.0 for Windows (Kaysville, UT). Differences among treatments were identified with Fisher's LSD multiple-comparison test ($P = 0.05$).

3. Results

3.1. In vitro effect of M. albus volatiles on P. digitatum and G. citri-aurantii

Growth of *P. digitatum* M6R and *G. citri-aurantii* plugs was completely inhibited during a three-day exposure to volatiles from a 7-day-old PDA culture of *M. albus*. At the end of the fumigation period, upon transfer to fresh PDA plates, all the plugs exposed to *M. albus* volatiles were confirmed dead while all the control plugs were viable (data not shown).

3.2. Control of green mold

In the first experiment, biofumigation was effective in controlling green mold regardless of the fumigation or pre-fumigation time after inoculation (Table 1). There was complete disease control if the fruit was fumigated immediately after inoculation, while a low level of infection could be found in fruit fumigated 24 h after inoculation. There was no significant difference in disease control among the various fumigation times. The incidence of green mold among the control fruit was 82%.

In the second experiment performed during the summer with more mature lemons, 100% of the control fruit were infected (Table 1). Although biofumigation

Table 1
Effect of fumigation with *M. albus* applied immediately or 24 h after inoculation on the incidence of green mold on lemons

Treatment	Green mold (%) after 7 days	
	Experiment 1	Experiment 2
Control	82.1 a	100.0 a
0 h post-inoculation		
24 h fumigation	0 b	10.7 c
48 h fumigation	0 b	5.5 c
72 h fumigation	0 b	0 c
24 h post-inoculation		
24 h fumigation	2.6 b	42.8 b
48 h fumigation	0 b	27.2 bc
72 h fumigation	2.6 b	30.4 b

Means followed by the same letter are not significantly different according to Fisher's LSD ($P = 0.05$).

significantly controlled green mold among all fumigation periods and inoculation intervals, the percentage of decay was higher than in the first experiment, probably reflecting the higher susceptibility to green mold infection of the more mature lemons. In this case, fumigation initiated immediately after inoculation was more effective than fumigation performed 24 h after inoculation. There were no significant differences among fumigation times.

In a test done with lemons inoculated with two inoculum concentrations (10^5 and 10^6 conidia/ml) and fumigated with different amounts of *M. albus* culture for a 24-h period beginning 24 h after inoculation, biofumigation was more effective under moderate disease pressure (Fig. 1). However, there was a clear inverse relationship between the amount of *M. albus* and the percent decay for both low and high inoculum pressures. In this experiment, the 10^5 and 10^6 conidia/ml inoculum concentration resulted in 76 and 95% infection among the untreated control lemons, respectively.

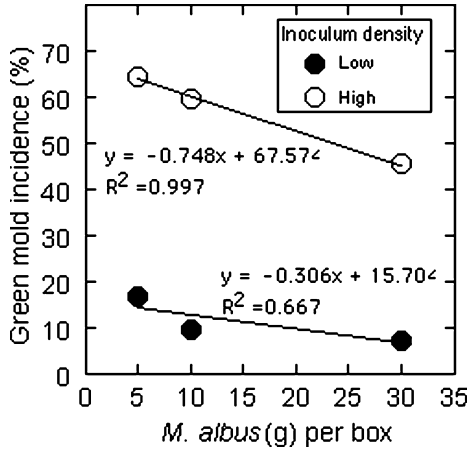

Fig. 1. Relationship between the amount of *M. albus* culture per box used for a 24 h fumigation applied 24 h after inoculation with *P. digitatum* and subsequent green mold incidence after 7 days. Low and high inoculum densities contained 10^5 and 10^6 conidia/ml, respectively.

3.3. Control of sour rot

In the first experiment, when the inoculum was supplemented with lemon juice, the inoculated control fruit had a low infection rate of about 31% (Table 2). There was nevertheless a significant reduction in sour rot when the 24 and 72 h fumigation periods were performed immediately after inoculation. In this case, the effect of a 48 h fumigation period was not significant. There was no disease control when biofumigation was initiated 24 h after inoculation.

In the second experiment, where disease pressure was increased by the addition of 10 ppm cycloheximide to the inoculum, 90% of control fruit were infected after 7 days. Results are shown for day 4 and day 7 (Table 3). With this high disease pressure, there was a significant disease reduction among all fumigation times longer than 24 h.

3.4. Room fumigation for green mold control

The biofumigation treatment during degreening reduced green mold among lemons within storage boxes in the first experiment from $92.7 \pm 4.2\%$ to $10.8 \pm 4.0\%$, a reduction of 88.3% in green mold incidence ($P = 0.01$). In the second experiment, the biofumigation treatment during degreening reduced green mold among lemons

Table 2
Effect of fumigation with *M. albus* applied immediately or 24 h after inoculation on the incidence of sour rot of lemons after storage for 14 days

Fumigation duration (h)	Sour rot (%) incidence
None	30.9 a
Immediately post-inoculation	
24	9.5 bc
48	14.3 ab
72	2.4 c
24 h post-inoculation	
24	28.6 a
48	21.4 ab
72	26.2 ab

Means followed by the same letter are not significantly different according to Fisher's LSD ($P = 0.05$).

Table 3
Effect of fumigation with *M. albus* applied immediately after inoculation on the control of sour rot of lemons after 4 and 7 days

Fumigation duration (h)	Sour rot (%) incidence	
	Day 4	Day 7
None	80.0 a	90.0 a
24	65.1 a	86.1 a
48	13.4 b	42.0 b
72	17.4 b	36.8 b
120	11.8 b	25.2 b

Lemons were inoculated with an arthrospore suspension that contained 10 ppm cycloheximide. Means followed by the same letter are not significantly different according to Fisher's LSD ($P = 0.05$).

within storage boxes from 86.9 ± 1.9% to 41.6 ± 5.7%, a reduction of 52.1% in green mold incidence ($P = 0.01$).

Results with fruit treated while in commercial fiberboard cartons were similar to those in open lemon storage boxes. In the second experiment, the biofumigation treatment during degreening reduced green mold among lemons within cartons from 92.9 ± 1.3% to 49.6 ± 7.4%, a reduction of 46.7% in green mold incidence ($P = 0.01$). The appearance of the lemons was not changed by the *M. albus* treatment, and the development of yellow color induced by ethylene treatment was similar between *M. albus*-treated and untreated lemons.

4. Discussion

Biofumigation with *M. albus* is a promising approach to control green mold of citrus, because relatively short fumigation times of 24–72 h controlled most wound infections, even when initiated 24 h after inoculation. These results are comparable to decay control by *M. albus* in apples and peaches using the same biofumigation conditions (Mercier and Jiménez, 2004). Because inoculum plugs of *P. digitatum* were killed in the in vitro fumigation assay, it is also likely that the pathogen was killed in wounds by the biofumigation treatment.

The difference in effectiveness between green mold control experiments can be explained by differences in fruit maturity, because the lemons in the second test were considerably more mature (softer and deeper yellow), which are more susceptible to the disease, than those of the first test. The superior wound healing ability and phytoalexin accumulation potential of the less mature fruit (Ben-Yehoshua et al., 1998) probably contributed to the efficacy of the biofumigation treatment. Light green to dark green lemons would always be treated in one commercial application that was simulated in this work, where lemons would be protected from decay during ethylene degreening by *M. albus* volatiles.

Biofumigation with *M. albus* also provided some control of sour rot, although to a lesser extend than green mold. In the case of sour rot, the treatment was not effective when applied 24 h post-inoculation. The use of cycloheximide in the second test considerably increased fruit susceptibility to *G. citri-aurantii* through the inhibition of the wound-healing process. Such inhibition of wound healing could have facilitated infection by surviving arthrospores during or after the treatment. However, even the partial control of sour rot by *M. albus* is useful because there are currently no effective means to control this disease. The reduced efficacy of *M. albus* volatiles against sour rot when compared to green mold or other postharvest diseases (Mercier and Jiménez, 2004) could be either due to a higher tolerance of *G. citri-aurantii* to the volatiles or an ability to escape exposure to them. While quantitative studies will be required to evaluate the sensitivity of individual pathogens to *M. albus* volatiles, the in vitro assay showed that *G. citri-aurantii* is indeed sensitive to the volatiles. The lack of disease control with biofumigation applied 24 h post-inoculation suggests that the pathogen could be escaping in the fruit tissues. Lesions caused by *G. citri-aurantii* contained gelatinous tissue from the macerated peel, which may have inhibited penetration of the volatiles. Further tests under conditions of natural inoculum could provide more answers about the potential of biofumigation to control sour rot.

Green mold control was good when biofumigation was performed in a room in conjunction with an ethylene treatment. Termed degreening, ethylene treatment is used accelerate the development of yellow or orange color in citrus fruit to improve their appeal to consumers (Reid, 2002). Particularly, when fruit are harvested during rainy periods, postharvest decay losses during degreening can be very high. Since the degreening process is applied before the fruit are processed on packinglines where fungicides are applied, they are often unprotected from pathogens during this process, which is applied at 20 °C in California, a temperature that facilitates the development of green mold and sour rot (Eckert and Eaks, 1989). There was no evidence of an interaction of ethylene with *M. albus* or its volatiles. We measured the surface color of lemons ($n = 40$) repeatedly during degreening with 5 ppm ethylene at 20 °C for 48 h and again 3 days later with a chroma meter (McGuire, 1992). The shift in color from green to yellow advanced normally among ethylene-treated fruit with or without *M. albus*, from an initial hue angle of about 116° to a final measurement of 100° 5 days later. The hue change of those in air was small, from 116° initially to 115°.

It is possible that some of infections that occurred among the biofumigated lemons that resided in bulk-loaded commercial lemons storage boxes or cartons happened because some of the fruit were not exposed to the volatiles, as the infection sites were located between contiguous fruit or against the sides of containers, a situation that did not occur in our small box tests where contact between fruit was prevented. Control of green mold within fiberboard cartons was as effective as that in open lemon storage boxes, which demonstrated that penetration of the volatiles into packed fiberboard cartons, which had relatively small vents, occurred. Differences in effectiveness between the ethylene degreening experiments are likely due to differences in potency in the *M. albus* rye culture used. In these experiments, the biofumigant rate of 0.85 g of dry rye culture per liter was calculated to treat an air volume of about 12,000 L and was in the same range found effective in small box tests (0.46–0.91 g/L) for control of blue mold of apple (J. Mercier, unpublished data). In the case of storage rooms filled with fruit with little remaining air volume to treat,

it is possible that a biofumigant/fruit biomass ratio could be a more accurate method to determine the use rate because fruit types vary in surface area and possibly in their ability to bind or break down volatiles.

Freshly harvested citrus in California are often treated with fungicides only after the degreening process, so considerable losses can occur during this process. Biofumigation during degreening could protect the fruit and could reduce the need for further disease control treatments afterward. Although not measured in this work, it is likely *M. albus* could also considerably abate the number of air-borne spores in degreening rooms and within storage facilities. During storage or shipping, biofumigation could also be applied for further decay protection if necessary, either within whole storage rooms, shipping containers, or in individual shipping boxes.

There was an inverse relationship between the amount of *M. albus* culture and percent green mold control in fruit inoculated with two conidial concentrations, indicating that disease control is directly related to the amounts of biofumigant used. Measurement of the three most abundant volatiles in the 11-L plastic boxes fumigated with 30 g of rye culture of *M. albus* revealed that ppb levels of isobutyric acid, isobutyl alcohol, and 2-methyl-1-butanol (24, 0.6, and 1.8 ppb detected after 24 h, respectively) were detectable throughout the fumigation process at ambient air temperature (Mercier and Jiménez, 2004). It is still unknown how much these volatiles account for disease control or whether they are just indicator of biofumigant activity. Other volatiles detected were mainly alcohol or ester derivatives of benign toxicity (Mercier and Jiménez, 2004; Strobel et al., 2001). There has been an interest in recent years in the use of natural compounds for the fumigation of fruit for disease control. One advantage of using volatiles is to be able to treat fruit without having to handle them. The principal compounds showing activity were isothiocyanates (Mari et al., 1996), acetic acid and other fatty acids (Sholberg, 1998; Sholberg et al., 2001), ethanol (Yuen et al., 1995) and ethereal compounds such as acetaldehyde and benzaldehyde (Caccioni et al., 1995; Yuen et al., 1995). In general, the concentration of natural volatiles required for disease control are considerably higher than the ones produced by *M. albus* and can result in off-flavors or phytotoxicity. Also their efficacy might not be sufficient to make their application practical. The mixture of *M. albus* volatiles, with its many components, could have synergistic properties that cannot be achieved by any single component alone (Strobel et al., 2001).

More research is needed on the relationship between volatile production and disease control, to determine more reliably the concentrations required for efficacy. Because of their extremely low concentrations, it is most likely that residues of *M. albus* volatiles in treated fruits are negligible or undetectable, which would make the treatment attractive from commercial and regulatory standpoints. The use of *M. albus* in citrus could be very flexible because it would be compatible with the various phases of the handling process, including degreening, storage in cold rooms, transport in containers, and fruit packaging. The treatment could be applied passively by simply placing active *M. albus* culture in the presence of the fruit. It could also reduce the need for postharvest fungicide drenching of bins or pre-harvest fungicide applications, which would be a further advantage of this treatment over most chemical or biological agents.

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